Structure and Function of Leaves, Plants and Ecosystems

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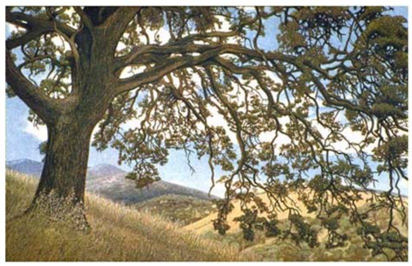
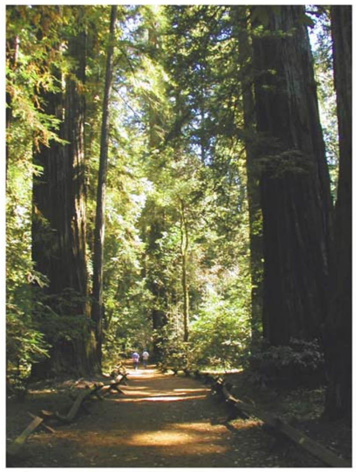


'Form Follows Function', Louis Henri Sullivan (1856-1924), architect



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'Form follows function—that has been misunderstood.
Form and function should be one, joined in a spiritual union',
Frank Lloyd Wright (1869-1959),
protégé' of Louis Henri Sullivan and architect

Quercus douglasii, 2 cm
Grows in Hot, dry Climate

Acer macrophyllum, 30 cm
Grows in Cool, Humid, Climate

Roles of Structure and Function

- Supporting Photosynthetic organs
  - Leaves and Plants
- Intercepting sunlight
  - Leaf size, shape, thickness, orientation and phenology
- Mining soil for water and nutrients
  - Roots, depth, architecture
- Increasing Reproductive Success
  - Flower color, type
  - Seed size and shape
  - Phenology, timing of flowering and leafing
- Facilitating the diffusion of CO_2 to Chloroplasts
  - Leaf thickness, Photosynthetic pathway, stomatal geometry,

Important Structural/Functional Attributes/Traits for classifying a Functional type include

- Physiognomy
  - Grass, Herb, Shrub, Tree
  - Broad-leaved vs. Needle-leaved Tree
  - Parallel vs Netted veined Herbs/Grasses
  - Fibrous vs. tap roots
- Life Span
  - Annual, Biennial, Deciduous, Evergreen
- Pollination and Seed dispersal
  - Insect, Wind
- Photosynthetic pathway
  - C_3, C_4, CAM
- Mychorrhizal Association
  - Endo/Ecto
- Tolerance Features
  - Drought, shade, fire, nutrient, frost, freeze, heat

Leaf and Plant Traits

- Leaf Form/Function
  - Size, Thickness and Shape, Longevity, Angle, Photosynthetic Pathway, Specific Leaf Area, Carbon and Nitrogen Content, Photosynthetic Capacity
- Plant Growth Form
  - Leaf area density, height, longevity, crown size, tolerance to stress
- Stem/Wood
  - Wood density, xylem conductivity

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New paper by Chave et al. 2009 Ecology Letter covers traits of wood

Broad Continuum of Leaf Shape and Size
How to Bring Order to Chaos? Do Rules Emerge?

Whitfield, 2006 Nature

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There is a diverse set of leaf sizes and shapes, up to 250,000 different combinations

??Do Species/Genera Matter, in Ecosystem Ecology??

With over 300,000 documented Plant Species,
How Do we Characterize the Key Functional and Structural Attributes
of Ecosystem Biodiversity in a Tractable Manner?

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Species are human constructs that tell us more about how organisms breed than metabolize. With the idea of functional convergence, different species doing the same thing, and the reality of thousands of species, focusing on species per se does not help us accomplish our task of knowing carbon, water and nutrient fluxes

Do Species/Genera Matter, in Ecosystem Ecology?

- Diversity in functional characteristics/traits better explains differences in the acquisition of mass and energy (light, water, net primary productivity, nutrients) rather than species diversity
  - The contribution of each species to ecosystem performance is not equal
    - (Tilman et al., 2001; Hooper et al., 2005)
- Ecosystem function is controlled by a combination of factors
  - Dominant & Keystone Species, Ecological Engineers and Species Interactions (competition, facilitation, mutualism, predation)

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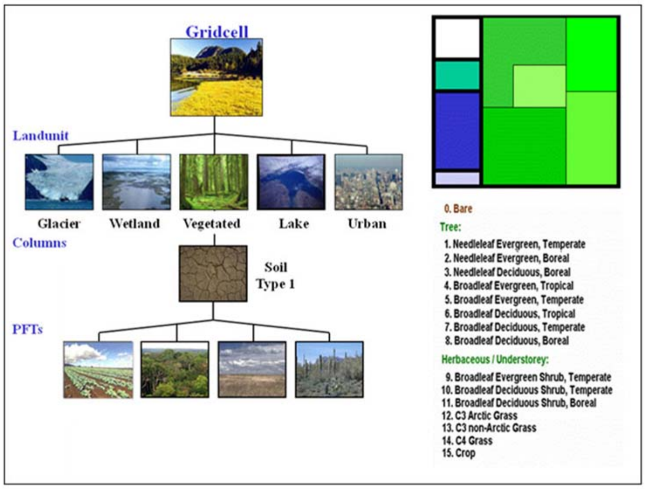
All species are not created equal, with regards to ecosystem exchange, energy, carbon, water and nutrient cycling.

Climate and Ecosystem Models adopt the Concept of Plant Functional Types



Too Coarse?; Too Simplistic?; Good Enough and Practical?

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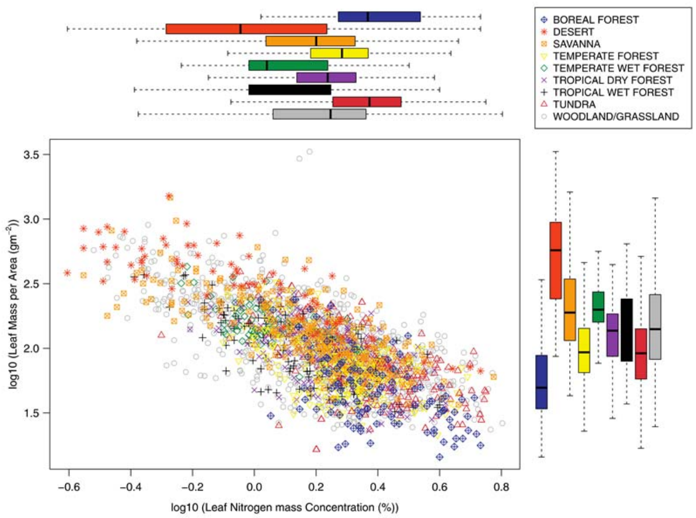
In the past few decades the idea of functional groups has gained traction for predicting ecosystem fluxes and ecosystem-climate interactions. The idea has been adopted mostly by climate and ecosystem modelers.

Plant Traits are Replacing Functional Groups as the Traits follow
A continuum and are less discrete. Plus Functional Groups have overlapping Traits



Von Bodegom et al 2012

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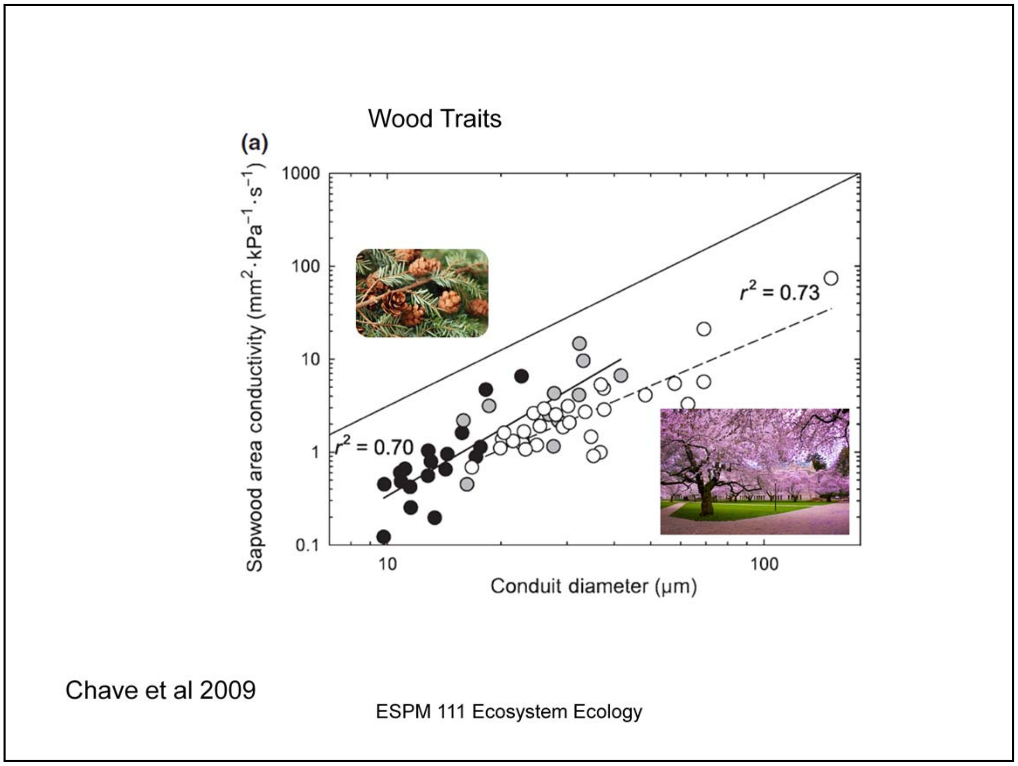
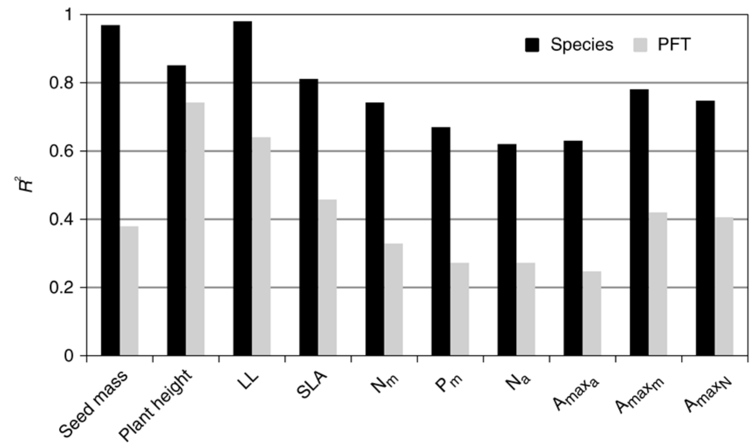
Von Bodegom et al 2012 Global Ecology and Biogeography. Trait information is more continuous and tells us more than information for discrete plant functional types. Plus the traits of functional groups overlap



Chave et al 2009 Ecology Letters functional traits of wood. Closed are gymnosperms; open are angiosperms

Traits are better than Functional Types



Kattge et al 2011 GCB

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The r2, the coefficient of determination, of traits explains more of the variance than plant functional groups. Emerging ideas as this course has evolved

Physiological Attributes of Plants

- **photosynthetic pathway**
  - C_3
  - C_4
  - CAM






Plants use one of three major metabolic pathways to assimilate carbon dioxide. The pathways are associated with the first fixed carbon compound in the carbon cycle. C3 is used by most plants, all trees, netted veined herbs and some grasses. C4 is the pathway used by many tropical grasses like corn and sugar cane. Cam is a pathway used by many desert succulents.

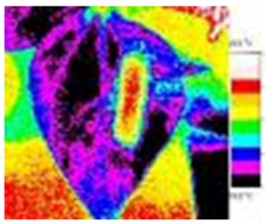
shape and **size** of leaves

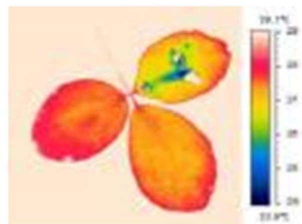
- needles vs planar vs shoots
- projected vs surface area of needles
- projected to total needle area
- Big vs Small
- Parallel vs Netted Veins




Leaf size, shape and orientation affect

- the properties of the **leaf boundary layer**;
- the **reflectance** and **transmittance** of light
- leaf's **energy balance**





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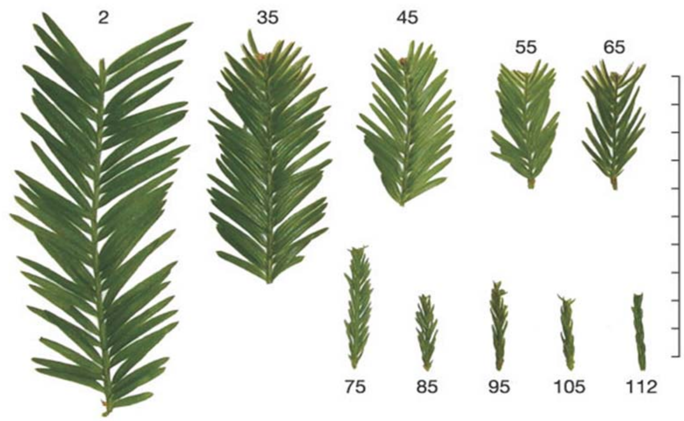
Size and shape of leaf will affect its energy balance and its temperature.

How Variable is Leaf Shape in an Ecosystem?; on an Individual?

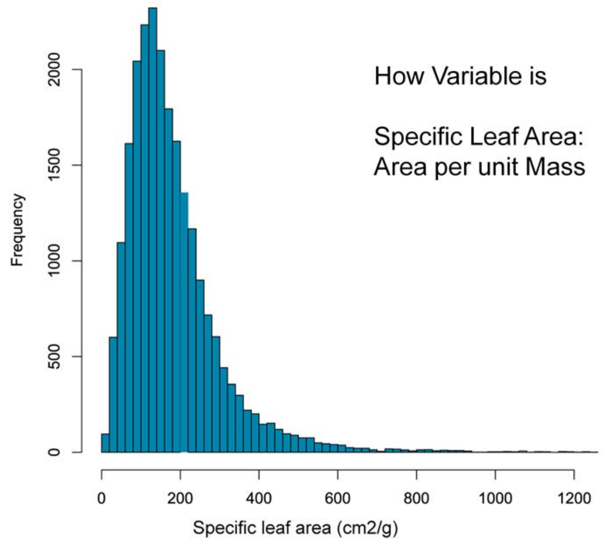


Vertical variation of redwood leaf morphology with height

Koch et al. 2004 Nature

The size and shape of shoots on a single organism or tree can be as diverse as across a landscape or ecosystems. Look at this case with redwoods

TRY Database

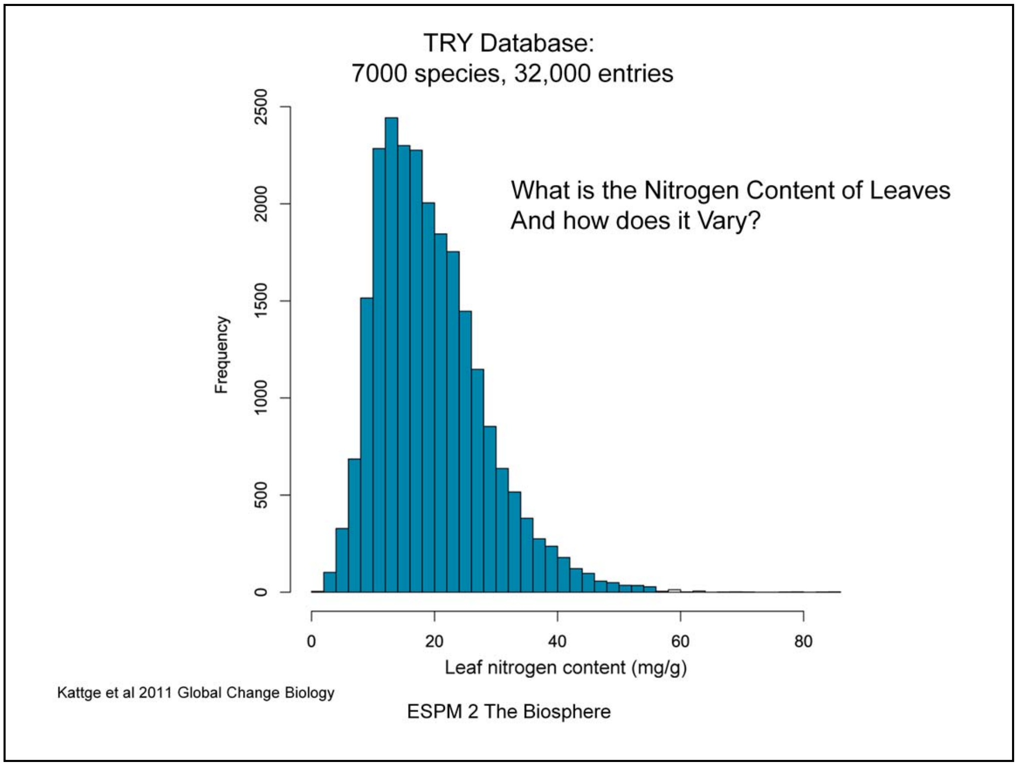


How Variable is

Specific Leaf Area:
Area per unit Mass

Kattge et al 2011 Global Change Biology

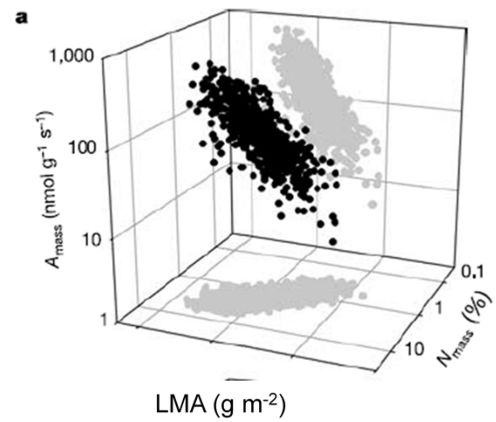
ESPM 2 The Biosphere

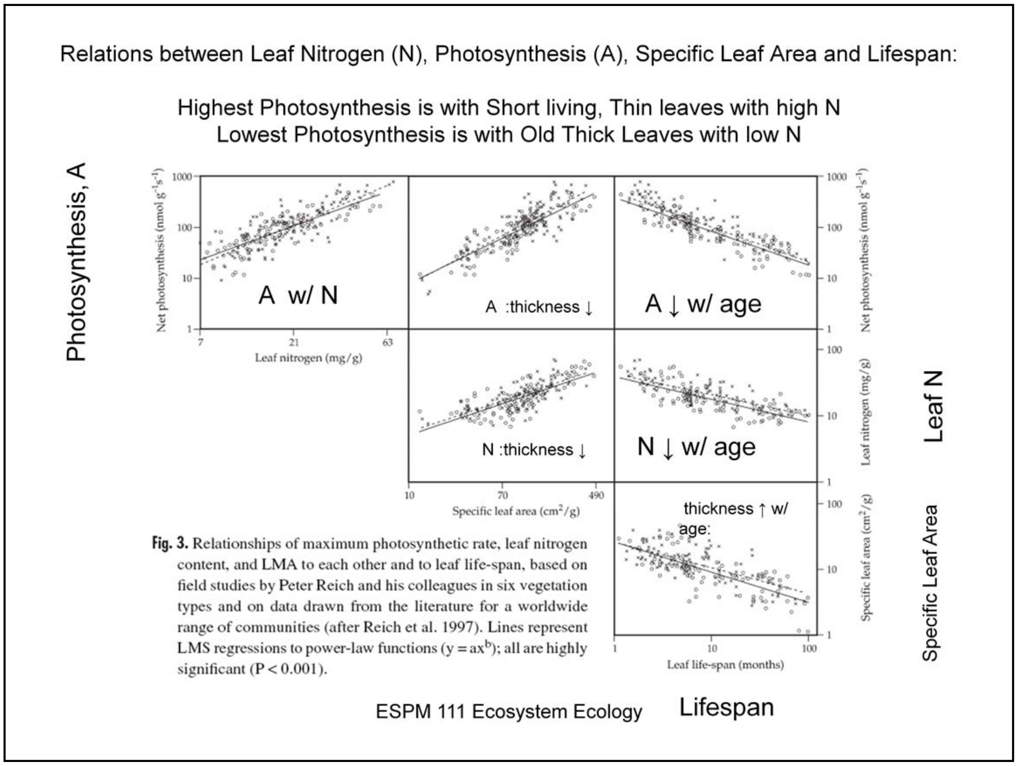

TRY Database:
7000 species, 32,000 entries
What is the Nitrogen Content of Leaves
And how does it Vary?
Frequency
0
500
1000
1500
2000
2500
0
20
40
60
80
Leaf nitrogen content (mg/g)
Kattge et al 2011 Global Change Biology
ESPM 2 The Biosphere

Leaf Structure and Function:
Emerging Ecological Rules

85% of variation in photosynthesis (per unit mass) is explained by variations in leaf mass per unit area and leaf Nitrogen per unit mass

Wright et al, 2004 Nature



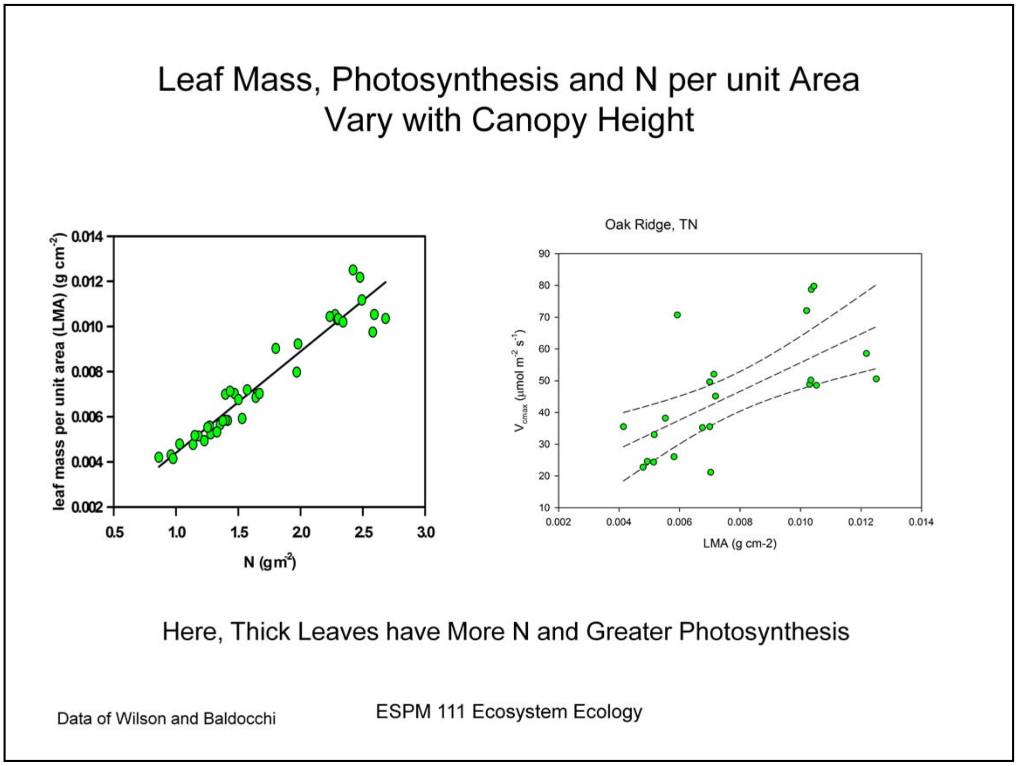


Highest Photosynthesis is with short living, thin leaves with high N…leaf economics
Lowest photosynthesis is with old thick leaves with low N

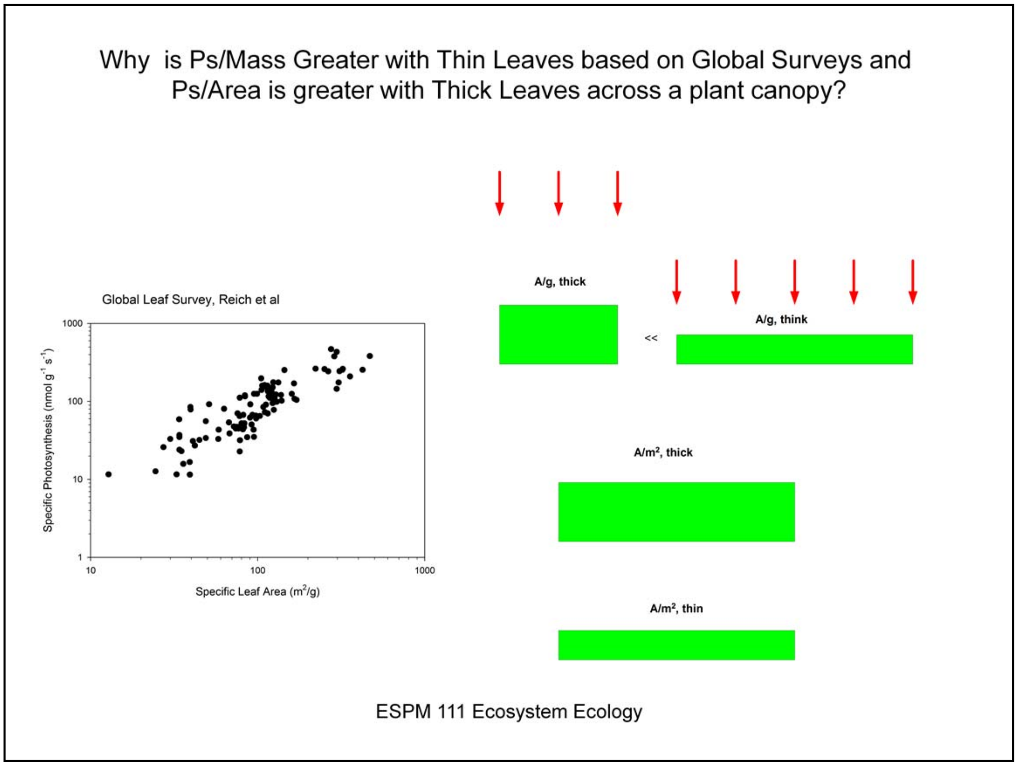
Concepts

- High Photosynthetic rates per unit Mass (A_{mass}) requires High level of Nitrogen, per unit mass (N_{mass})
  - The enzyme RUBISCO, which catalyzes the photosynthetic reactions contains much N and is ecologically ‘expensive’.
- But this requirement leads to vulnerability of herbivory and more respiration, which places limits on Specific Leaf Area
  - Insects need to eat N heavy compounds to produce proteins.
- Leaf longevity is correlated with Specific Leaf Area (or low mass per unit area) because
  - Longer living leaves must be tougher and have low palatability
  - Fast growing leaves shade older inferior leaves
- Effects of climate on leaf traits were modest

Wright et al, 2004 Nature

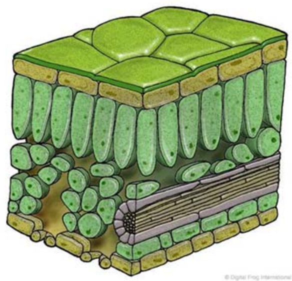


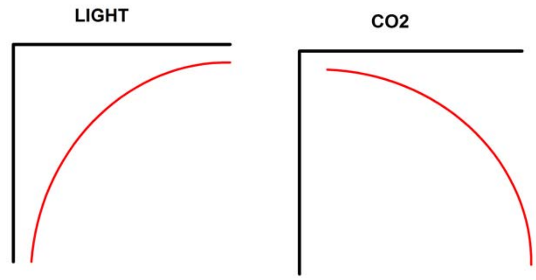
Alternatively if we assessing scaling relationship through the vertical confines of a forest canopy we find that leaf nitrogen and photosynthetic capacity are functions of and increase with leaf thickness, quantified in terms of mass per unit area.



It is critical to assess these scaling relationships on both area and mass bases to understand their behavior

Classic Question:
How Thick Can or Should a Leaf Be?





The Thicker the Leaf, More Chlorophyll for Photosynthesis; Too Thick And All Light is Intercepted and CO2 Diffusion through the Mesophyll is Inhibiting, causing a Draw-Down in CO2 and Negative Feedback on Photosynthesis

Physical Attributes of Plant Canopies

- **leaf area index**
  - – amount of leaf area per ground area (m^2 m^{-2})
- **woody biomass area index**
  - – silhouette woody biomass per unit area

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At the canopy scale we are concerned with leaf area index, meters of leaves per meter of soils

Range of LAI Values

Functional type	Mean LAI	Std Dev
Polar desert/alpine tundra	3.85	2.37
Moist tundra	.82	.47
Boreal forest woodland	3.11	2.28
Temperate savanna	1.37	.83
Temperate evergreen broadleaved forest	5.4	2.32
Temperate mixed forest	5.26	2.88
Temperate conifer forest	6.91	5.85
Temperate deciduous forest	5.3	1.96
Temperate wetland	6.66	2.41
Cropland Temperate	4.36	3.71
Plantation Temperate	9.19	4.51
Tall medium grassland	2.03	5.79
Short grassland	2.53	.32
Arid shrubland	1.88	.74
Mediterranean shrubland	1.71	.76
Tropical wetland	4.95	.28
Tropical savanna	1.81	1.81
Tropical evergreen rain forest	5.23	2.61
Tropical deciduous forest	4.67	3.08
Tropical pasture	2.85	2.62
Crop tropical	3.65	2.14
Plantation tropical	9.91	4.31

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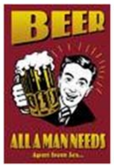
Asner et al 2003

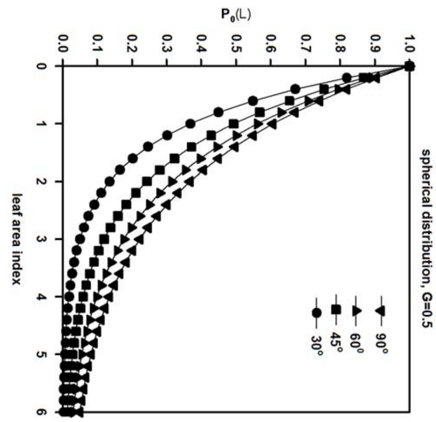
LAI ranges between 10 and 1 and there are family of values associated with different functional types

How Much Leaf Area is Possible?



Beer's Law

$$I / I_0 \approx P_0 \approx \exp(-kL)$$



I, transmitted sunlight
I_0, incident sunlight
k, extinction coefficient
L, leaf area index

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Beer's law helps us understand the upper limit of possible leaf area index. It is not physically and biologically reasonable to establish more layers of leaves if most of the incoming light has been absorbed.

~Maximum Light Attenuation, 95% Yields 5% Light Transmission through the Canopy: $I/I_0=0.05$

$$L = -\ln(0.05) / 0.5 = 6$$

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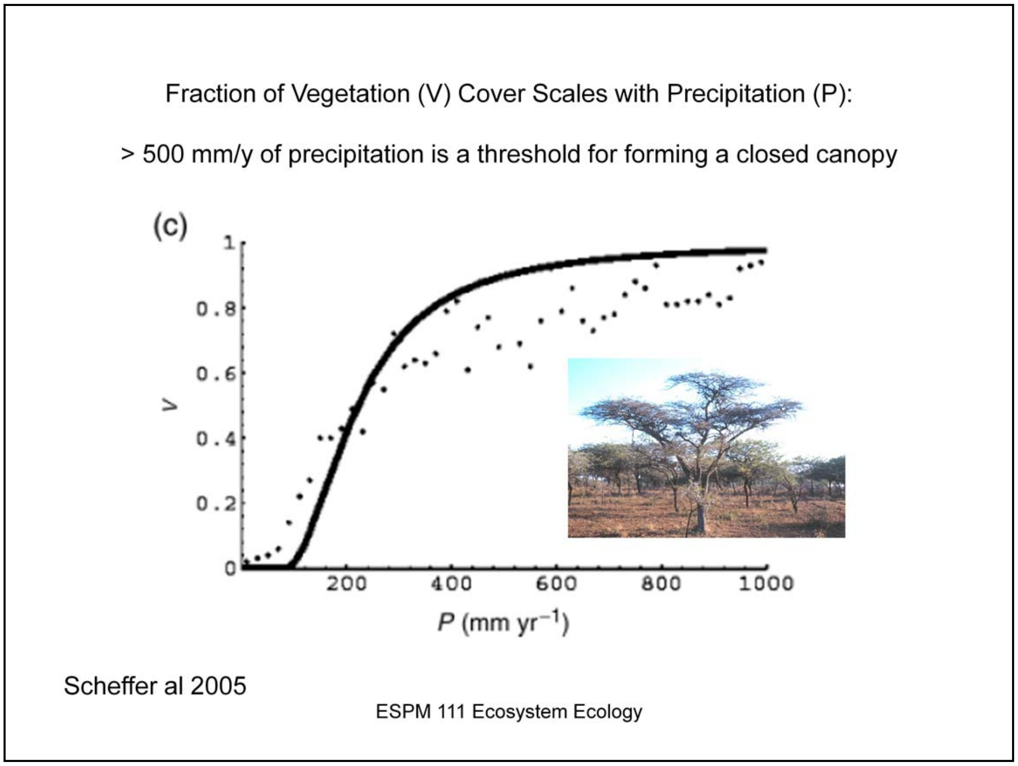
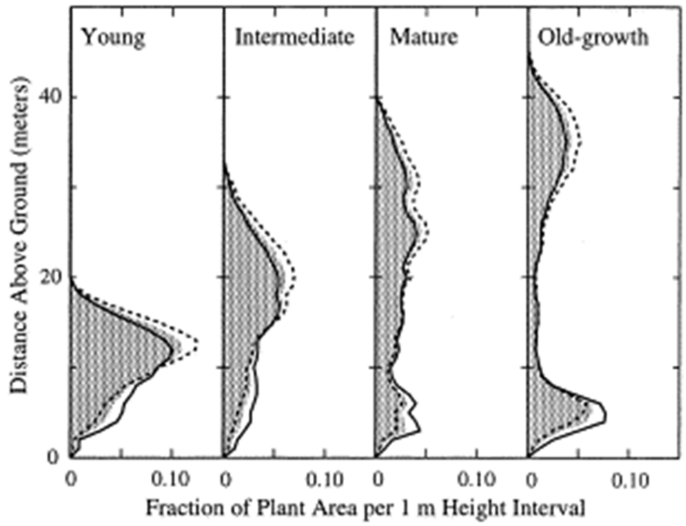
6 m2/m2 is the typical upper limit of LAI for most humid forests. Plantations tend to attain higher values, with management (also watch for bad data).



Water is the factor limiting lai, too. Scheffer et al. 2005

LAI Profile by Stand Age



Aber et al., 1979

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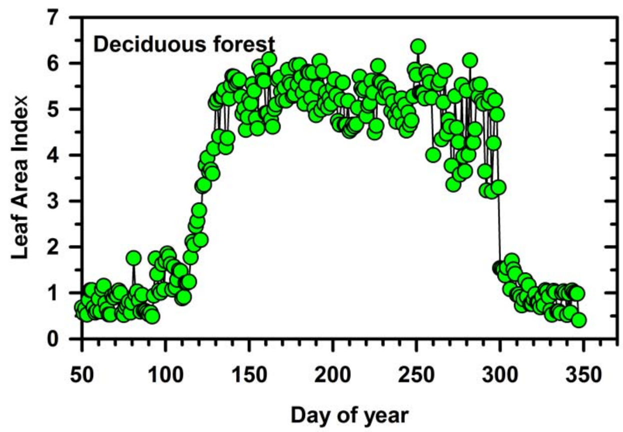
The vertical variation of LAI is different for different forest age classes. Intermediate age forests tend to exclude light to the understory. As forests age, tree fall occurs and gaps promote understory growth, hence the bimodal distribution

Attributes of Ecosystems

- **Plant Habit**
  - Deciduous/Evergreen
  - Woody/Herbaceous
  - Annual/Perennial

Seasonality in LAI, Deciduous Forests



Transition between Leafless and Full-leaf states is Rapid

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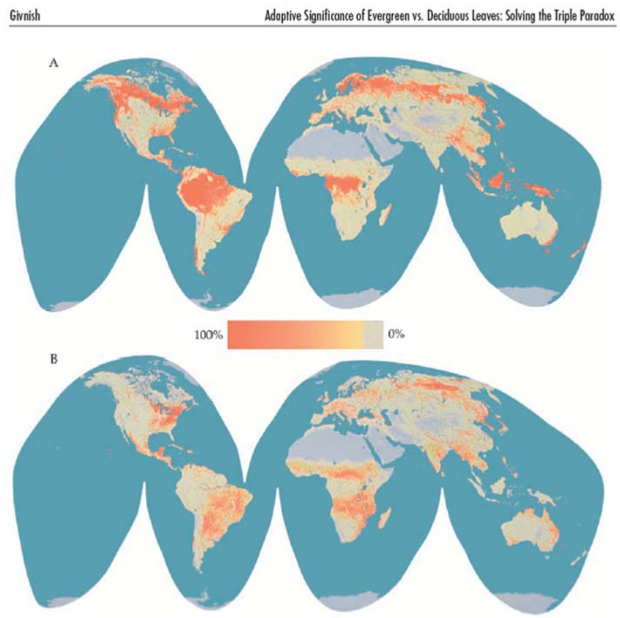
In deciduous forests, LAI is not constant and experiences much seasonality. After Baldocchi and Wilson

Evergreen Forests

Deciduous Forests



Givnish 2002 Silva Fennica

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Evergreen/Deciduous Pros/Con

Evergreen	**Deciduous**
Long photosynthetic season	Higher Ps per unit mass
Lower amortized cost of construction	No respiration and transpiration during unfavorable season
Lower amortized cost of replacing leaf nutrients	Lower root cost
Tougher laminae, able to withstand freeze, frost, herbivory	

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Poor soils favor evergreen due to depressed Ps capacity, which can be overcome with long growing season; Temperate-humid climates with long growing seasons favor evergreen, eg Pacific Northwest

Vertical Attributes of Plants

- **canopy height**
  - **Trees**
    - **Redwoods,~ 80m**
    - **Hardwood forest, ~ 30 m**
  - **Shrubs**
    - **Savanna, ~10m**
    - **Chaparral, ~3 m**
  - **Grasses**
    - **Corn, ~3m**
    - **Grass, ~ 0.1 m**
  - **Herbs**
    - **Soybeans, ~1m**

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How tall can vegetation get and for different functional types?

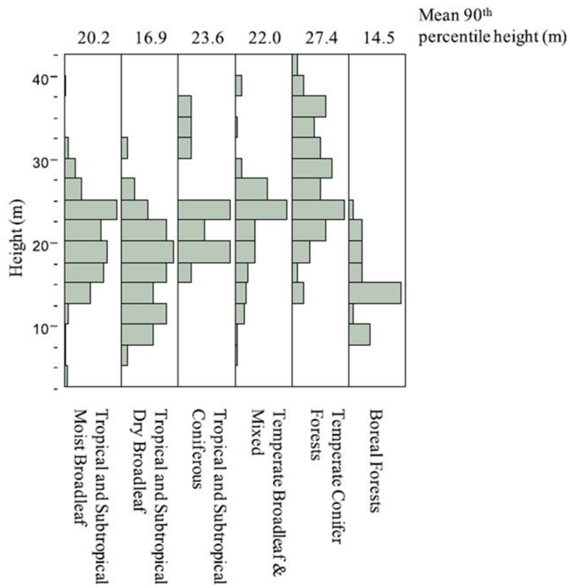

Figure 2. Distribution of heights for six broad forest classes.

Lefsky 2010 GRL

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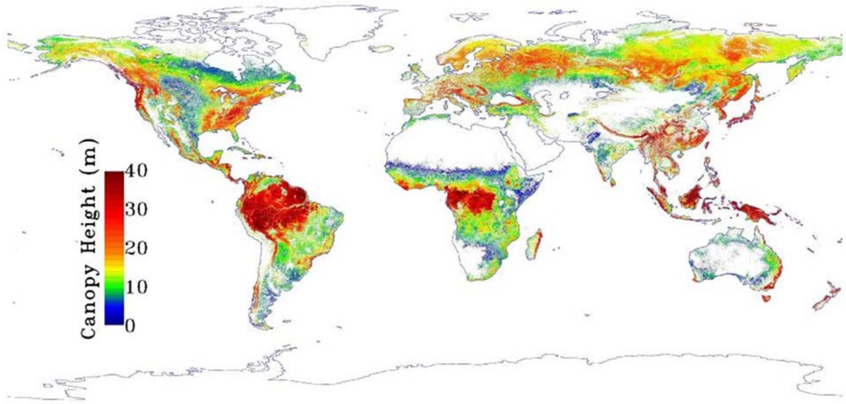
LIDAR is giving us new tools to measure tall forests well and with higher statistical sampling

Global Map of Canopy Height

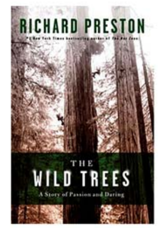


Simard et al 2011 JGR Biogeoscience

LIDAR on a satellite measuring ice was recently used to map tree height across the world. Hopefully better sensors will improve this first map,

What Limits the Height of Trees?

- Respiration Hypothesis
  - Larger Organisms respire more, so they grow less
  - Classic textbook explanation
  - But respiration declines with decline in growth
- Nutrient Limitation Hypothesis
  - Sequestration of nutrients in Biomass limits growth
- Hydraulic Limitation Hypothesis
  - Water potential decreases with increasing plant height, leading to restrictions in stomatal opening and photosynthesis
  - Supported by many studies, but not all
- Wind Load
  - Tall plants vulnerable to wind throw



leaf angle distribution

- **Erectophile**
- **Planophile**
- **Spherical**
- **Azimuthally symmetric or asymmetric**

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Leaves have different angular inclinations in different environmentsl

Variable Leaf Angles on Blue Oak

Photo: Youngryel Ryu

Leaf Angles Vary with Depth in a Closed Broadleaved Forest:

Leaves in the upper canopy are quasi-erect
Leaves in the subcanopy are horizontal

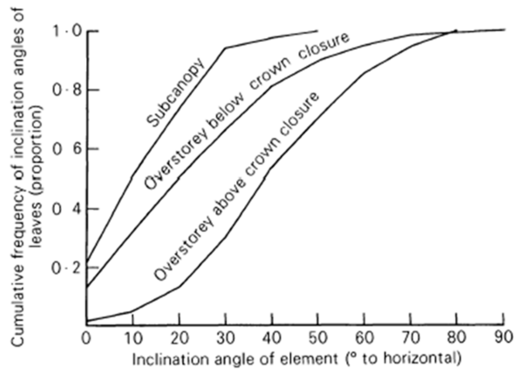

FIG. 3. Cumulative area-weighted frequency distributions of the inclination angles of leaves in the three major strata of a deciduous forest in eastern Tennessee, U.S.A.

Hutchison et al., 1986, J Ecol

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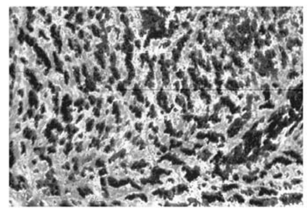
The angle of leaves in a forest are more erect near the top and flat near the ground.

Horizontal (spatial) distribution

- **Leaves**
  - Random dispersion
  - Clumped dispersion
  - Regular dispersion
- **Plants**
  - Random
  - Rows
  - Clumped



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Clumping

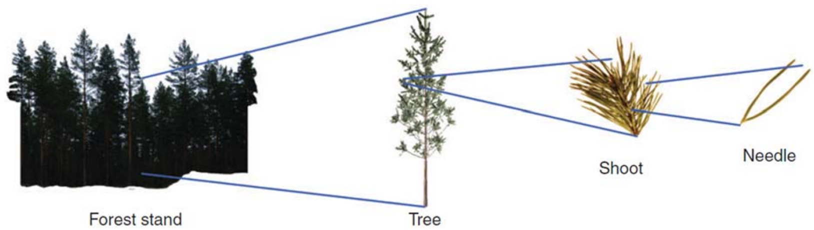

FIG. 1. The different structural levels used in describing the structure of a coniferous stand.

Clumping occurs across different spatial scales and affects light transmission

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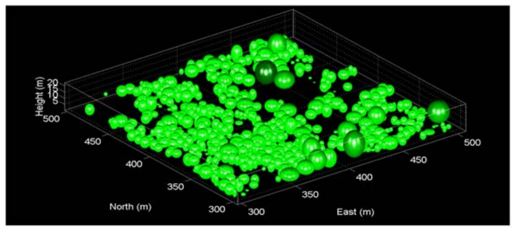
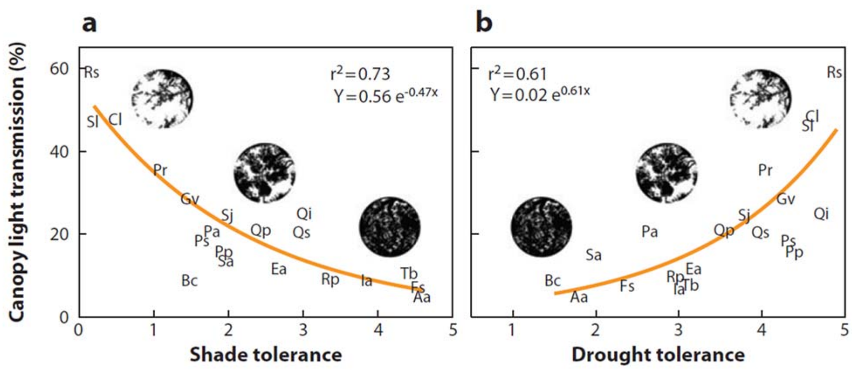
Clumping is a 'new' trait that a sub-group of biometeorologists are focusing on. It affects the efficacy of light transmission through plant canopies and is now being quantified with LIDAR and gap fraction measurements

Spatial attributes of Plant Canopies

- **crown volume** and **shape**
- **plant species**
- **stem density**
- **spatial distribution** of plants



Trade-Offs between Shade and Drought Tolerance



Valladares and Niinemets 2008, Ann Rev Ecol

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Plants that are shade tolerant are not drought tolerant, and vice versa.

Constraints on Resource Use by Plants

- *Premise I.*
  - *A plant that can photosynthesize at* high rates and grow rapidly under conditions of high light is unable to Survive at Low-Light levels (i.e., it is shade-intolerant).
  - A plant that is able to grow in low light (shade-tolerant plant) has a low maximum rate of growth and photosynthesis even under high light conditions

Smith and Huston, 1989 Vegetatio

Smith and Huston 1989, Vegetatio

Constraints on Resource Use by Plants

- *Premise 2.*
  - *A plant that can grow rapidly and/or* abundantly under conditions of high available soil moisture is unable to survive under dry conditions (i.e., it is intolerant to low moisture).
  - A plant adapted to survive and reproduce under dry conditions is unable to grow rapidly and/or reproduce abundantly even with high soil moisture availability (tolerant to low moisture)

Smith and Huston, 1989, Vegetatio

Constraints on Resource Use by Plants

- Tolerances to conditions of low light and low moisture are interdependent and inversely correlated. Adaptations that allow a plant to grow at low light levels restrict its ability to survive under dry conditions.
- Adaptations that allow survival under dry conditions reduce the plant's ability to grow in low light. Thus no woody plant can simultaneously have a high tolerance for low levels of both resources.

Multiple Resource Limitation in Ecosystems

- Plants adjust resource acquisition to maximize capture of the most limiting resource
  - Changes in Root/shoot allocation occurs
- Changes in the environment change the relative abundance of resources, so different factors limit NPP at different times
- Plants exhibit mechanisms that increase the supply of the most limiting resource
  - E.g. Symbiotic relation with N fixers
- Different resources limit different species in an ecosystem

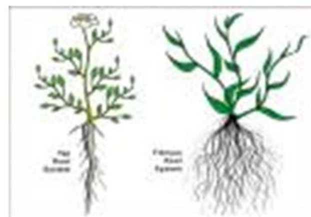
Chapin et al.

Survival in Extreme (hot, dry) Environments

- Acclimation
  - Shift in temperature response
- Adaptation/Endurance
  - Reflective leaves
  - Reduction in leaf size
  - Develop deep root systems
  - Store Water
  - Restrict stomatal conductance or hydraulic conductance
- Avoidance
  - Endure summer drought as seeds
  - Open Stomata at Night, eg. CAM Photosynthetic pathway

Physical Attributes of Roots

- **rooting** depth
- root architecture
  - Fibrous
  - Tap



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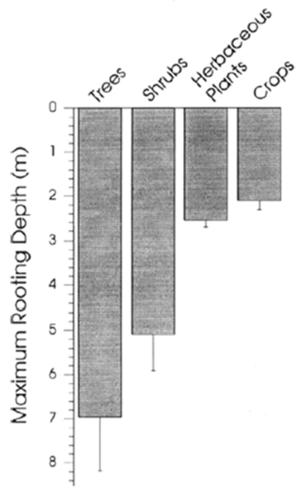
Maximum Rooting Depth

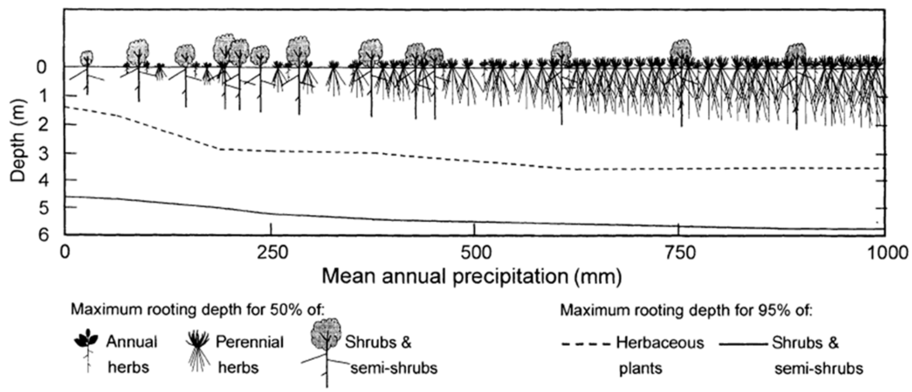


Canadell et al., 1996 Oecologia

Summary

- Physical attributes of a canopy include
  - leaf area index
  - canopy height
  - leaf size.
- Physiological attributes of a canopy include
  - photosynthetic pathway
  - stomatal distribution (amphi or hypostomatous)
- The physical and physiological attributes of a canopy can vary
  - in space (vertically and horizontally)
  - in time (seasonally and decadally).

Root Depth, Plant Functional Type and Climate



Schenk and Jackson 2002 J Ecol

What are mychorrhizae?: Root Fungi

•These fungi are obligate symbionts that form a mutual relationship with plant roots known as mycorrhizae.

•The fungi can receive between 3 and 22% of gross primary production (GPP) from their host plants in exchange for nutrient transfer to roots that benefit plant growth.

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Rodriog vargas

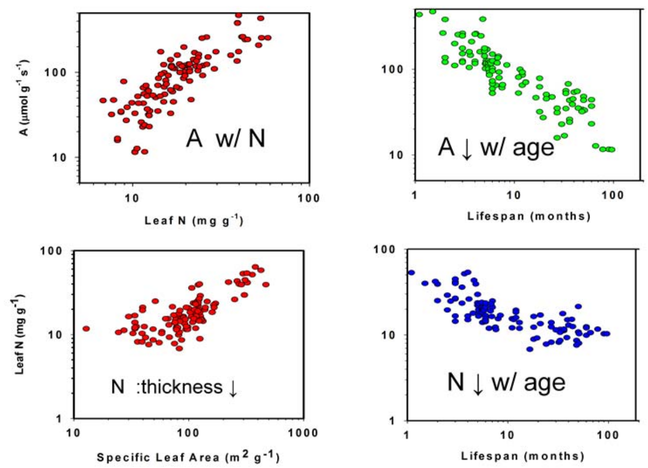
Summary

- Structural and functional properties of plant canopies alter:
  - wind and turbulence within and above the canopy, by exerting drag;
  - the interception and scattering of photons throughout the canopy;
  - the heat load on leaves and the soil;
  - the physiological resistances to water and CO_2 transfer
  - the biochemical capacity to consume or respire
  - carbon dioxide.

Points to Ponder

- What factors cause Evergreen and Deciduous trees to co-exist in CA?
- Does biodiversity and species matter when considering plant microclimates and mass and energy exchange?
- How has the Evolution of the Earth's climate affected the evolution of plant physiognomy and ecosystem structure and function?

Relations between leaf nitrogen, photosynthesis, specific leaf weight and lifespan:
Highest Photosynthesis is with short living, thin leaves with high N



adapted from Reich et al. 1997, PNAS,

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Thick leaves cannot support high A because of light attenuation and mesophyll resistance; old leaves cannot have high N due to herbivory

Leaf Size and Extinction

- Major Extinction at Triassic-Jurassic Boundary during period of Elevated Greenhouse effect
  - 4 fold increase in CO_2
  - 3 to 4 C temperature increase
  - 99% species turnover of megaflora with leaves > 5 cm
  - 10% species turnover of flora with leaves < 0.5 cm
  - Small Leaves are more effective in transferring heat and experiencing lethal surface temperatures

McElwain et al Science, 1999

Hydraulic Limitation Revisited

- Hydraulic limitation of gas exchange with increasing tree size is common, but not universal
- No evidence supports the original expectation that hydraulic limitation of carbon assimilation is sufficient to explain observed declines in wood production
- Any limit in height does not appear to be related to age-related decline in wood production

Ryan et al 2006, PCE

L15401 LEFSKY: A GLOBAL FOREST CANOPY HEIGHT MAP L15401

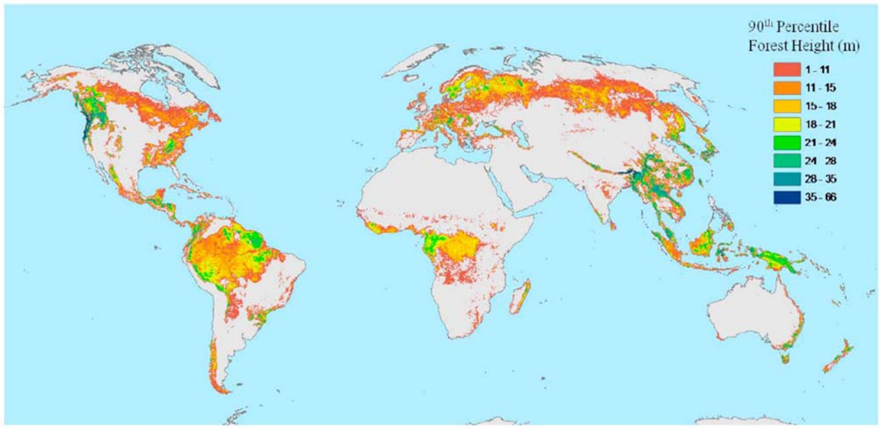

Figure 1. Global forest height map. Heights are the 90th percentile of GLAS height observations within a patch.